

Da cooperação entre Max-Planck-Institut für Limnologie, Arbeitsgruppe Tropenökologie, Plön, Alemanha Oc., e Instituto Nacional de Pesquisas da Amazônia, Manaus – Amazonas, Brasil

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## The larval development of palaemonid shrimps from the Amazon Region reared in the laboratory.

### IV. Abbreviated development of *Palaemonetes ivonicus* HOLTHUIS, 1950 (Crustacea: Decapoda)

by

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#### Abstract

The larval development of the freshwater shrimp *Palaemonetes ivonicus* was studied under laboratory conditions, based upon offsprings of ovigerous females collected in a várzea lake of the Solimões River system. The females carry few (12 to 43), large ( $2.31 \pm 0.14 \times 1.49 \pm 0.09$  mm), yolk-rich eggs. The species goes through three larval stages without feeding. The newly-hatched larva has sessile eyes and all the appendages, except for the uropods; however, some of the appendages still exhibit a rudimentary form. Larva II has stalked eyes and functional walking legs. Larva III has free uropods. Metamorphosis occurs between four and six days after hatching. Descriptions and illustrations of the larval and first juvenile stages are given.

Key words: Crustacea, Palaemonidae, *Palaemonetes ivonicus*, larval development, Amazon Region.

#### Resumo

O desenvolvimento larval em cativeiro do camarão dulcícola *Palaemonetes ivonicus* foi estudado a partir da prole de fêmeas ovadas coletadas em um lago de várzea do rio Solimões. As fêmeas carregam poucos ovos (12 a 43), sendo eles grandes ( $2,31 \pm 0,14 \times 1,49 \pm 0,09$  mm) e ricos em vitelo. A espécie apresenta três estágios larvais e não ingere alimento durante essa fase. A larva recém-eclodida apresenta olhos sésseis e todos os apêndices, com a exceção dos urópodos; alguns apêndices, entretanto, ainda exibem um aspecto rudimentar. A larva II apresenta olhos pedunculados e pernas ambulatórias funcionais. A larva III possui urópodos livres. A metamorfose ocorre entre quatro e seis dias após a eclosão. Descrições e ilustrações dos estágios larvais e primeiro estágio de juvenil são fornecidos.

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## Introduction

The freshwater shrimp *Palaemonetes ivonicus* was originally described from the Beni River, in Bolivia (HOLTHUIS 1950). Later, it was recorded in the Central Amazonian Region (HOLTHUIS 1966), where it is relatively common in the várzea lakes of the Solimões/Amazon River system, usually found among the roots of the floating aquatic macrophytes.

Several species of freshwater shrimps occurring in the Amazon basin present an abbreviated or extremely abbreviated larval development (GAMBA 1980; MAGALHÃES & WALKER 1984; VEGA 1984; MAGALHÃES in press; MAGALHÃES submitted). In the genus *Palaemonetes*, abbreviated development was fully described and illustrated for *P. paludosus* (by DOBKIN 1963) and *P. cummingi* (by DOBKIN 1971). Besides these papers, SOLLAUD (1923) briefly described or made comments on the abbreviated development of some species of this genus, and SHEN (1939, cited by DOBKIN 1963) reported this type of development also in *P. sinensis*. The present paper provides detailed morphological descriptions, along with illustrations, of the three larval and first juvenile stages of *P. ivonicus*, and also offers information on some life history characteristics.

## Material and Methods

In September 1983 and May 1984, several ovigerous females of *Palaemonetes ivonicus* were collected in Janauacá lake, about 70 km from Manaus, on the right bank of the Solimões River. They were brought to the laboratory in 100 l fiberglass containers filled with water from the lake and some aquatic plants. The procedures in the laboratory with the ovigerous females, for rearing the larvae, for dissecting and preparing the specimens for illustration, and for the measuring of eggs and shrimps were the same as explained in MAGALHÃES (in press). However, food was not offered during the larval phase. For greater clarity, plumes of plumose setae have been omitted in the drawings of the whole animal; where plumes are represented, they can be denser and longer than is indicated.

Some of the females, larvae and juveniles that were used in this study are deposited in the "Coleção Sistemática de Invertebrados, Seção Crustacea" of the Instituto Nacional de Pesquisas da Amazônia.

## Results

It usually takes two days for a female to release all of the clutch, and hatching was never observed during daytime. The total length (TL) of 20 ovigerous females was  $28.7 \pm 2.5$  mm and they carried 12 to 43 eggs (mean :  $26 \pm 10$ ). The eggs were elliptical and yolk-rich, with a mean size of  $2.31 \pm 0.14 \times 1.49 \pm 0.09$  mm ( $n = 20$ , from five specimens).

This species goes through three larval stages. The larvae are rich in yolk and do not feed until metamorphosis. Most of the larvae attained the juvenil phase in five days, but metamorphosis was accomplished as early as four days by some individuals. The various patterns of duration of the three larval stages are shown in figure 1.

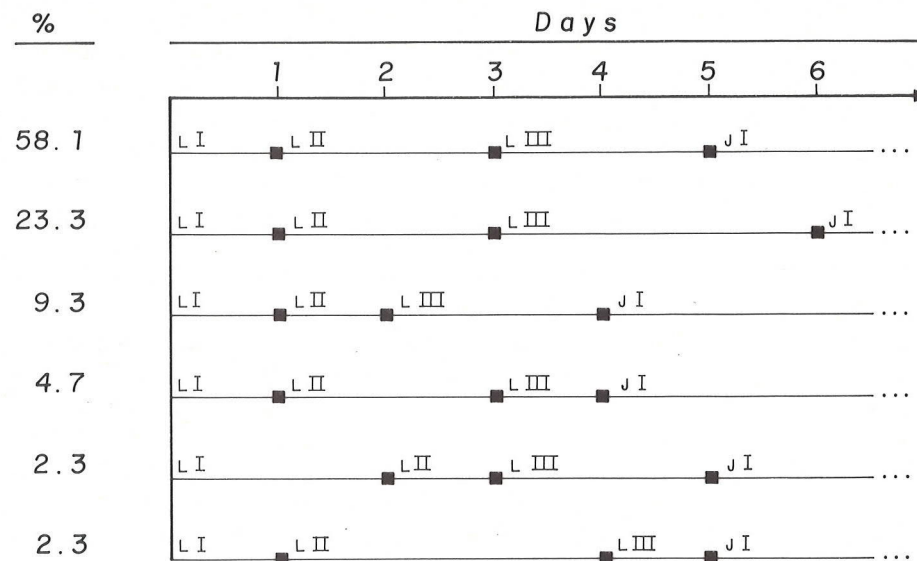


Fig. 1:  
Patterns of duration of the larval stages in *Palaemonetes ivonicus* ( $n = 43$  observations; L = larva; J = juvenile; square = molt).

## Description of the larval stages and juvenile I

### Body

**Larva I** (TL  $4.55 \pm 0.14$  mm;  $n = 21$ ; 4.29 to 4.88 mm) (Figs. 2, 3):

Rostrum smooth and short, straight or slightly curved downwards. Carapace with a spine on the antero-ventral corner; many specimens also have another oblique spine on the anterior border, just above the first one. Eyes sessile, with a distinct lobe anteriorly. Abdomen smooth, 6-segmented; pleuron of the 4th and 5th somites with a median notch on the latero-posterior border.

**Larva II** (TL  $4.70 \pm 0.19$  mm;  $n = 20$ ; 4.29 to 5.09 mm) (Figs. 20, 21):

Rostrum with a small dorsal tooth in some individuals. Carapace with a small supra-orbital spine. Eyes stalked; anterior lobe of the ocular peduncle reduced, but still visible. Abdomen without noteworthy differences.

**Larva III** (TL  $4.90 \pm 0.12$  mm;  $n = 20$ ; 4.66 to 5.04 mm) (Figs. 35, 36):

Rostrum with 1 (usually) or 2 dorsal teeth. Carapace and abdomen with no differences. Ocular peduncle with no trace of the anterior lobe.

**Juvenile I** (TL  $5.27 \pm 0.32$  mm;  $n = 25$ ; 4.77 to 6.12 mm) (Figs. 43, 44):

Rostrum a little longer, rostral formula 2-3/0-1. Carapace with only the antennal and branchiostegal spines.



### Antennule

**Larva I** (Fig. 4): Antennular peduncle unsegmented, but joints visible under the cuticle. Distally, with an inner plumose seta and an outer flagellum bearing 2 distal aesthetes and 1 subdistal short plumose seta.

**Larva II** (Fig. 22): Peduncle 3-segmented. Proximal segment with several, short and long, plumose setae as illustrated, a small spine on the disto-lateral corner, a small triangular spine ventrally and a rudimentary, rounded stylocerite. Median segment with a dorsal circlet of 5 short plumose setae terminally, 1 short plumose seta on the outer side and 2 long plumose setae on the inner side. Distal segment with a developed antennular lobe bearing 5 short weakly plumose setae, and 3 long ventral plumose setae subterminally. Distally, with a bisegmented inner flagellum now present; outer flagellum with 2 terminal aesthetes, 1 long subterminal naked seta and 2 other naked setae.

**Larva III** (Fig. 37): Stylocerite more prominent, statocyst beginning its development. Inner flagellum as long as the outer flagellum. The latter now subdivided, inner branch tipped with 3 aesthetes, outer branch with 2 apical short naked setae.

**Juvenile I** (Fig. 45): Stylocerite sharp; statocyst more developed. Short plumose setae increased in number. Inner flagellum 3-segmented and longer than the outer flagellum. The latter with the basal joint now distinct, the ramification being after this joint; inner branch shorter and tipped with 2 aesthetes, outer branch now bisegmented.

### Antenna

**Larva I** (Fig. 5): Protopod unsegmented, with a ventral spine on the distal border. Scale with 21 - 25 plumose setae along inner and distal margins and a spine on the disto-lateral corner. Endopod as a long, multi-articulated flagellum, about 4.6 - 5.3 times as long as the scale.

**Larva II** (Fig. 23): Protopod bisegmented; coxa with a small ventral epipod. Scale with 26 - 28 marginal plumose setae.

**Larva III and Juvenile I** (Fig. 46): Without noteworthy differences.

### Mandibles

**Larva I** (Figs. 6, 7): With molar and incisor processes not clearly defined.

**Larva II** (Figs. 24, 25): Incisor and molar process slightly separated; molar process broadly rounded; incisor narrower, with some small denticles in the right mandible.

**Larva III** (Figs. 38, 39): Incisor and molar processes more cleft; incisor process with small teeth; molar process rounded in the left mandible and subquadrate, with some small denticles, in the right mandible.

**Juvenile I** (Figs. 47, 48): Molar process subquadrate, with sharp and rounded teeth and several median denticles.

### Maxillula

**Larva I** (Fig. 8): Rudimentary. Endopod, coxal and basal endites smooth.

**Larvae II** (Fig. 26) **and III**: Still rudimentary. Endopod bilobed; coxal and basal endites with small protuberances terminally and subterminally.

**Juvenile I** (Fig. 49): Fully developed. Coxal endite now with 7 terminal weakly plumose setae and 1 inner small naked seta; basal endite with 12 spiniform, naked and weakly plumose, setae terminally, and 2 small setae (1 plumose and 1 naked) on the inner margin. Endopod with upper lobe rounded and lower lobe incurved, bearing a minute spine.

### Maxilla

**Larvae I** (Fig. 9), **II and III**: Protopod bilobed; both endites devoid of setae. Endopod with a small apical plumose seta on the first stage, which is absent in the other two larval stages. Scaphognathite large, with 33 - 36 marginal plumose setae.

**Juvenile I** (Fig. 50): Protopod with the lower and upper endites bearing, respectively, 3 and 4, naked and weakly plumose, setae. Endopod with a subterminal small plumose seta.

### Maxilliped 1

**Larva I** (Fig. 10): Protopod with inner margin simple and with a small epipod on the outer margin. Endopod with variable number of setae, bearing up to 3 terminal plumose setae and 1 outer naked and 1 inner plumose, subterminal setae. Exopod with 4 terminal long plumose setae and 1 subterminal short naked seta.

**Larva II** (Fig. 27): Protopod now with inner margin bilobed and epipod larger, digitiform. Endopod smooth.

**Larva III** (Fig. 40): Basal endite with 2 small naked setae. First third of the exopod with a small protuberance and slightly bulged.

**Juvenile I** (Fig. 51): Coxal endite with 2 plumose and 1 naked setae; basal endite with 17, naked and weakly plumose, setae terminally and subterminally; epipod large and subtriangular. Exopodal lobe more bulged, with 5 plumose setae.

### Maxilliped 2

**Larva I** (Fig. 11): Protopod smooth, with a faint segmentation between coxa and basis. Endopod with 4 well-defined segments; penultimate segment with 2 very long weakly plumose setae, the median setae being exceedingly long and naked proximally; distal segment with an outer minute naked seta proximally, 2 weakly plumose and 1 naked seta subterminally, and a terminal spine plumose only on the inner side. Exopod with 6, terminal and subterminal, plumose setae.

**Larva II** (Fig. 28): Protopod bisegmented; coxa with a small epipod. Endopod distinctly 5-segmented; penultimate segment with setae very much reduced, not over-reaching the end of the distal segment. Distal segment usually with 3 short plumose setae and 1 terminal spine.

**Larva III** (Fig. 41): Endopod distinctly incurved; penultimate segment wider and smooth; distal segment subtriangular, bearing some protuberances and up to 7, naked and plumose, setae.

**Juvenile I** (Fig. 52): Coxa with a little larger epipod on the outer margin and 2 naked setae on the inner margin. Endopod with penultimate segment bearing 4 - 5 weakly plumose setae (2 - 3 on the inner margin and 2 on the distal margin). Distal segment wider than long, bearing several naked and weakly plumose setae terminally and subterminally.



### Maxilliped 3

**Larva I** (Fig. 12): Protopod bisegmented, smooth. Endopod 4-segmented; proximal segment with a long weakly plumose seta; penultimate and distal segments with 1 naked and 1 weakly plumose setae each, distal segment also with a long and strong terminal spine bearing plumes on its distal half. Exopod with 4 plumose setae terminally and 1 naked and 1 plumose seta subterminally.

**Larvae II** (Fig. 29) and **III**: Basis with 3 short naked setae on the inner margin. Endopod 5-segmented, with 1, 1 - 2, 1, 2 - 3, 2 - 3, naked and plumose setae from the proximal to the distal segment; terminal spine much reduced.

**Juvenile I** (Fig. 53): Coxa with 1 naked seta on inner margin. Endopod now 3-segmented, bearing several naked and weakly plumose setae, mainly on the inner side of the joints. Exopod unchanged.

### Pereiopods 1 and 2

**Larva I** (Figs. 13, 14): Well-developed, biramous buds. Protopod unsegmented. Endopod chelate, with faint segmentation. Exopod short, devoid of setae.

**Larvae II** (Figs. 30, 31), and **III**: Protopod bisegmented. Endopod 5-segmented; a few short naked setae are scattered from coxa to dactyl. Exopod with 6 - 7 naked and plumose setae terminally and subterminally. Pereiopod 1 with 1 (larva II) and 3 (larva III) short plumose setae on the proximal inner side of the palm.

**Juvenile I** (Figs. 54, 55): Still biramous, but with exopod much reduced and smooth (it will disappear with succeeding molts). All segments with some short, naked and plumose, setae; a tuft is present at the tip of both fixed and movable fingers. Pereiopod 1 with the characteristic oblique subterminal row of 4 plumose setae on the inner side of the carpus and 3 spiniform plumose setae on the inner proximal side of the palm.

### Pereiopods 3, 4 and 5

**Larva I** (Figs. 15, 16, 17): All as well-developed, uniramous buds. Segmentation absent or slight, except between the protopod and the endopod, which is clearly marked.

**Larvae II** (Fig. 32), **III** and **Juvenile I** (Fig. 56): Morphologically, all similar and fully developed. Protopod bisegmented. Endopod 5-segmented, with a short terminal spine; several short, naked and weakly plumose, setae are scattered on the segments, mainly in the propodus.

### Pleopods 1 - 5

**Larva I** (Fig. 18a - e): Small, biramous, smooth buds.

**Larvae II** (Fig. 33a - e) and **III**: More developed buds, with rudimentary appendices internae.

**Juvenile I** (Fig. 57a, b): Fully developed. Exopods with several marginal plumose setae and 1 subterminal naked seta. Endopods with 2 marginal plumose setae and the appendices internae bearing a minute hook (except in pleopod 1, whose endopod is the shortest, bearing no setae).

### Uropod

**Larvae I** (Fig. 19) and **II** (Fig. 34): Not yet freed; buds visible through the telson cuticle.

**Larva III** (Fig. 42): Protopod with the outer distal corner rounded. Exopod developed, with a disto-lateral spine, 17 - 19 plumose setae along most of the inner and posterior margins, 2 minute plumose setae on the outer proximal border, and some short, naked and plumose, setae on the dorsal and ventral (these were not represented in the drawing) surfaces. Endopod rudimentary, smooth.

**Juvenile I** (Fig. 58): Outer distal corner of the protopod sharp. Exopod with an increased number of marginal and superficial setae. Endopod developed, with 12 marginal plumose setae, 5 short weakly plumose setae on the outer proximal margin and several others on the dorsal surface (those setae that lay ventrally to other structures were not represented in the drawing).

### Telson

**Larvae I** (Fig. 19) and **II**: Broadly triangular; posterior margin with a slight median concavity and bearing 8 + 8 (usually), 9 + 8 or 9 + 9 plumose setae.

**Larva III** (Fig. 42): Narrower in its first half, but its posterior part still very wide; posterior margin with 7 + 7 (usually), 8 + 8 or 8 + 7 plumose setae and median concavity bearing 2 minute spines; disto-lateral corner with a small spine.

**Juvenile I** (Fig. 58): Somewhat rectangular, lateral margins almost parallel; posterior margin with 5 + 5 (usually) or 6 + 5 setae (the outermost pair naked, the remainder plumose) and median concavity more pronounced, with 2 minute spines; disto-lateral margin with 3 small spines.

### Color of the larvae

The larvae are transparent to the naked eye, but a light greenish hue can be noted in the cephalothorax. Red chromatophores are present in the ocular peduncle, the antennular peduncle, the antenna, the lateral region of the carapace, the dorsal region of the 2nd to 6th abdominal segments, near the base of the maxillipeds and pereiopod 3, and between the pleopods. Black chromatophores are present in the cephalothoracic region, the ocular peduncle, the antenna, the buccal region, some joints of the pereiopods, near the base of the pleopods, along the posterior margin of the abdominal segments, the telson (near the anus and the posterior margin), and the posterior margin of the uropods.

The chromatophores are more evident in the first and second larval stages, but the individuals become progressively more colorless with succeeding molts.

### Preserved material

Brazil, State of Amazonas, Janauacá lake, 08. ix. 1983, C. Magalhães, 05 females whose larvae hatched in the laboratory, INPA-CR 216; idem, 17. v. 1984, INPA-CR 217; Manaus, INPA Aquaculture Station, ix. 1983 and v. 1984, C. Magalhães, 05 larvae I, 14 larvae II, 02 larvae III, 11 juveniles I, INPA-CR 221.



## Discussion

The larval development of *Palaemonetes ivonicus* is similar to that described for *P. paludosus* (by DOBKIN 1963) and *P. cummingi* (by DOBKIN 1971), mainly in terms of the type of development. All these species have only three larval stages and bear, on hatching, all the appendages except for the uropods, which are freed only at the third larval stage. Morphologically, however, there are several differences, and some structures of *P. ivonicus* are, on hatching, a little more advanced than the corresponding ones in *P. paludosus* and *P. cummingi*. This is the case for the 6th abdominal somite, that is clearly separated from the telson in *P. ivonicus* but is not in the other two species. Similarly, in *P. ivonicus* the antenna bears a scale with many marginal plumose setae and an endopod with a long, multi-articulated flagellum, while in *P. paludosus* and *P. cummingi* the antennal flagellum is unsegmented and shorter than the scale.

At the end of the larval phase, the mandibles, maxillulae and maxillae of *P. ivonicus* show the basic adult plan but are not functional and bear no developed teeth or setae (with the exception of the scaphognathite). At least in *P. paludosus*, these structures bear teeth and setae, but resemble morphologically those of the species with long larval development. The development of the pereopods are similar in the above three species, particularly the chelipeds. However, in *P. ivonicus* the walking legs are uniramous during the larval phase, while in the larvae of the other two species the pereopod 3 is still biramous. Also the development of the tail is similar in these species, but the number of plumose setae on the posterior margin of the telson is a little greater in *P. ivonicus*.

Other *Palaemonetes* with larval development similar to those discussed above are *P. antennarius* (as *P. varians lacustris*) and *P. mesogenitor* (as *P. punicus*), both partially studied by SOLLAUD (1923). The former, like *P. ivonicus*, has uniramous pereopod 3 during the larval phase, but the latter has all the pereopods, even the chelipeds, uniramous on hatching.

The larval development of *P. ivonicus* exhibits two very peculiar features in the first larval stage: the anterior lobe of the sessile ocular peduncle, and the exceedingly long seta in the endopod of maxilliped 2. This seta becomes very much reduced in the following stage and it is difficult to know if it has some special function. In the free-swimming larvae of palaemonid shrimps with long larval development the endopods of the maxillipeds are normally used to capture and handle suspended food particles, but *P. ivonicus*' larvae are not planktonic and do not feed. This species is commonly found in várzea lakes associated with floating macrophytes and a possible reason for this long seta might be to help the larva cling to the substratum formed by their roots. In the second larval stage, the pereopods 3 - 5 are already functional and could take on this task.

*P. ivonicus* exhibits no variability in the number of larval stages but the duration of each larval stage can vary (Figure 1). In most cases, the larva I lasts one day and larvae II and III two days each. The structures show only slight variations and these are restricted to the number and/or to the condition of some setae: they can be either present or absent, developed or rudimentary, plumose or naked. Sometimes, some setae can be present in a certain structure on the right side of the body and absent on the left side.

Two other *Palaemonetes* are reported for the Amazon basin. From these, it is already known that *P. mercedae* has an almost direct development consisting of only one larval stage (MAGALHÃES, submitted). The postembryonic development of *P. carteri*, however, has not been fully studied yet. A brief account given by SOLLAUD (1923: 577 - 578, fig. XX), based on the morphology of an advanced embryo of *P. carteri* (as *P. cubensis*, according to HOLTHUIS 1952), suggests that this species has a larval development resembling that of *P. ivonicus*.

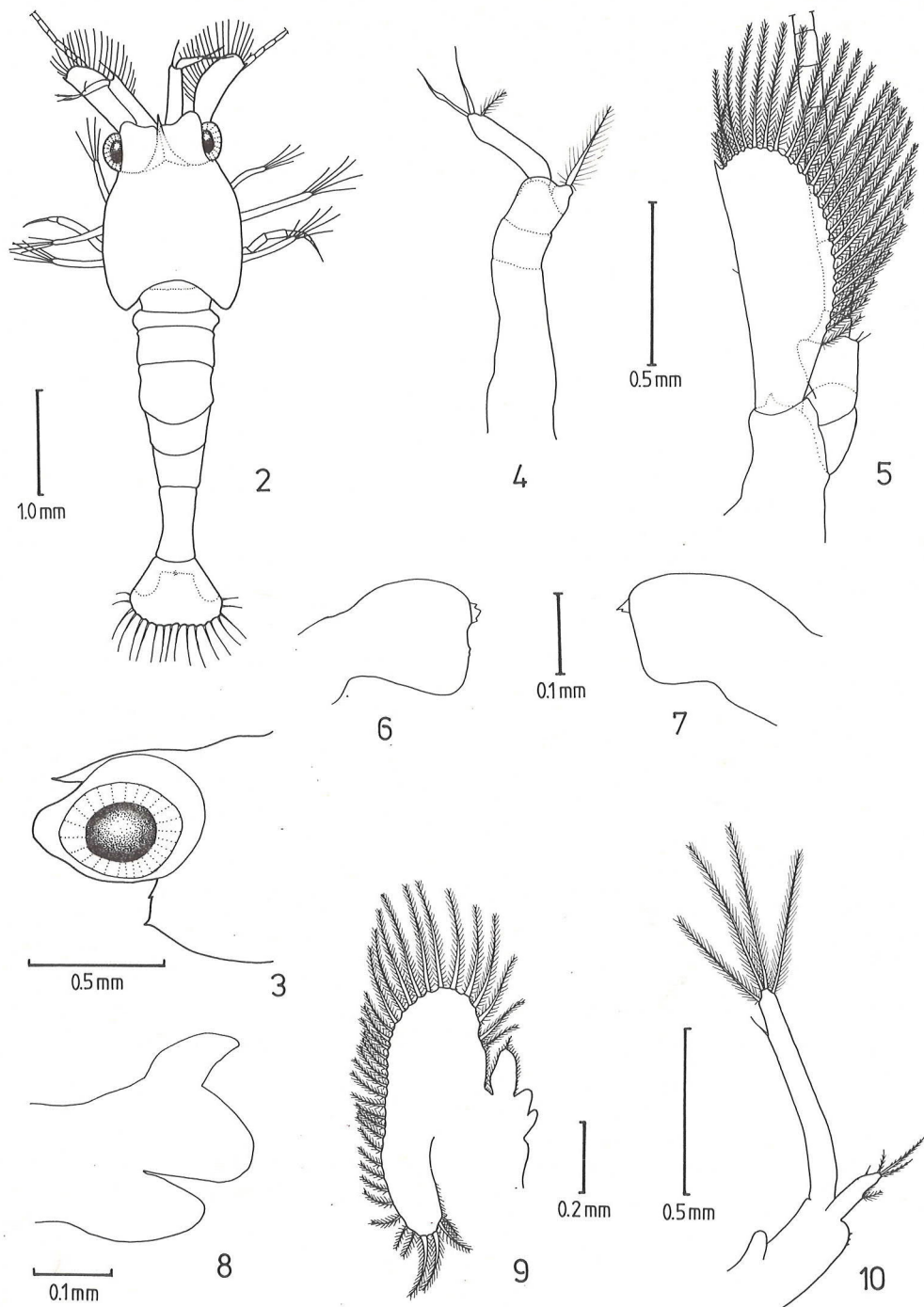
## Acknowledgments

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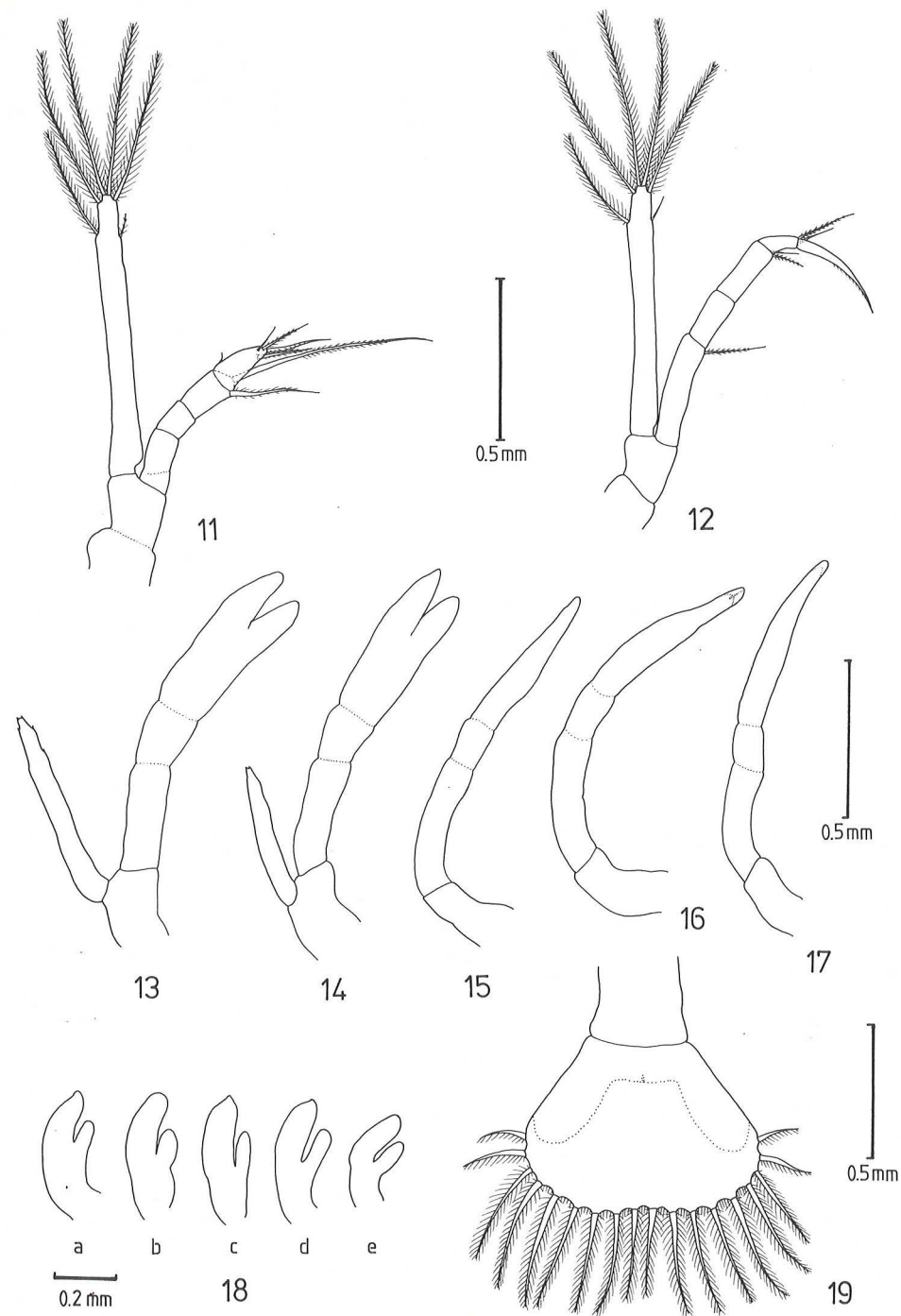




Figs. 2 - 10:

*Palaemonetes ivonicus*, larva I:

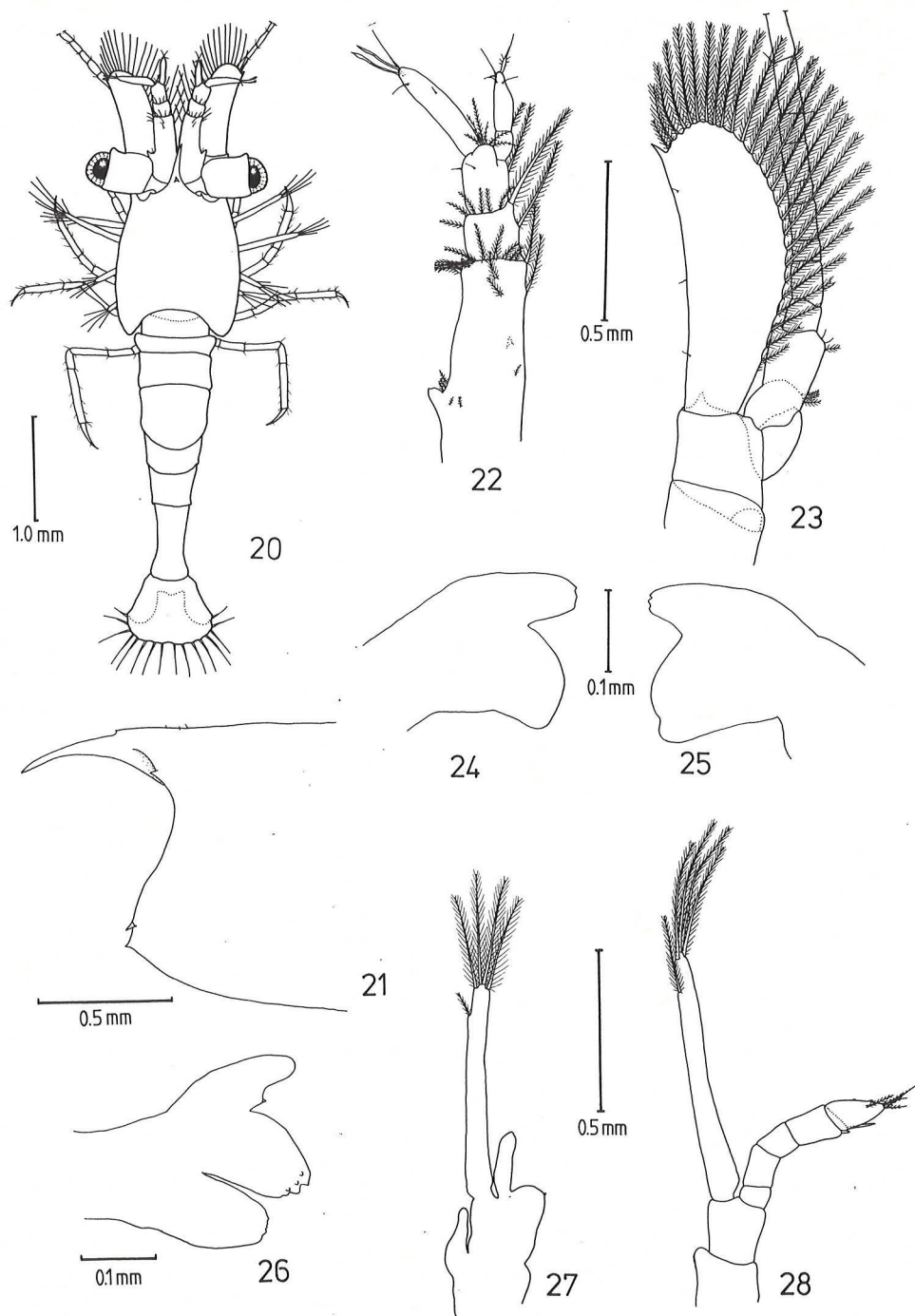
2: Dorsal view; 3: Lateral view of the anterior part of the carapace and eye; 4: Antennule; 5: Antenna; 6: Left mandible; 7: Right mandible; 8: Maxillula; 9: Maxilla; 10: Maxilliped 1.



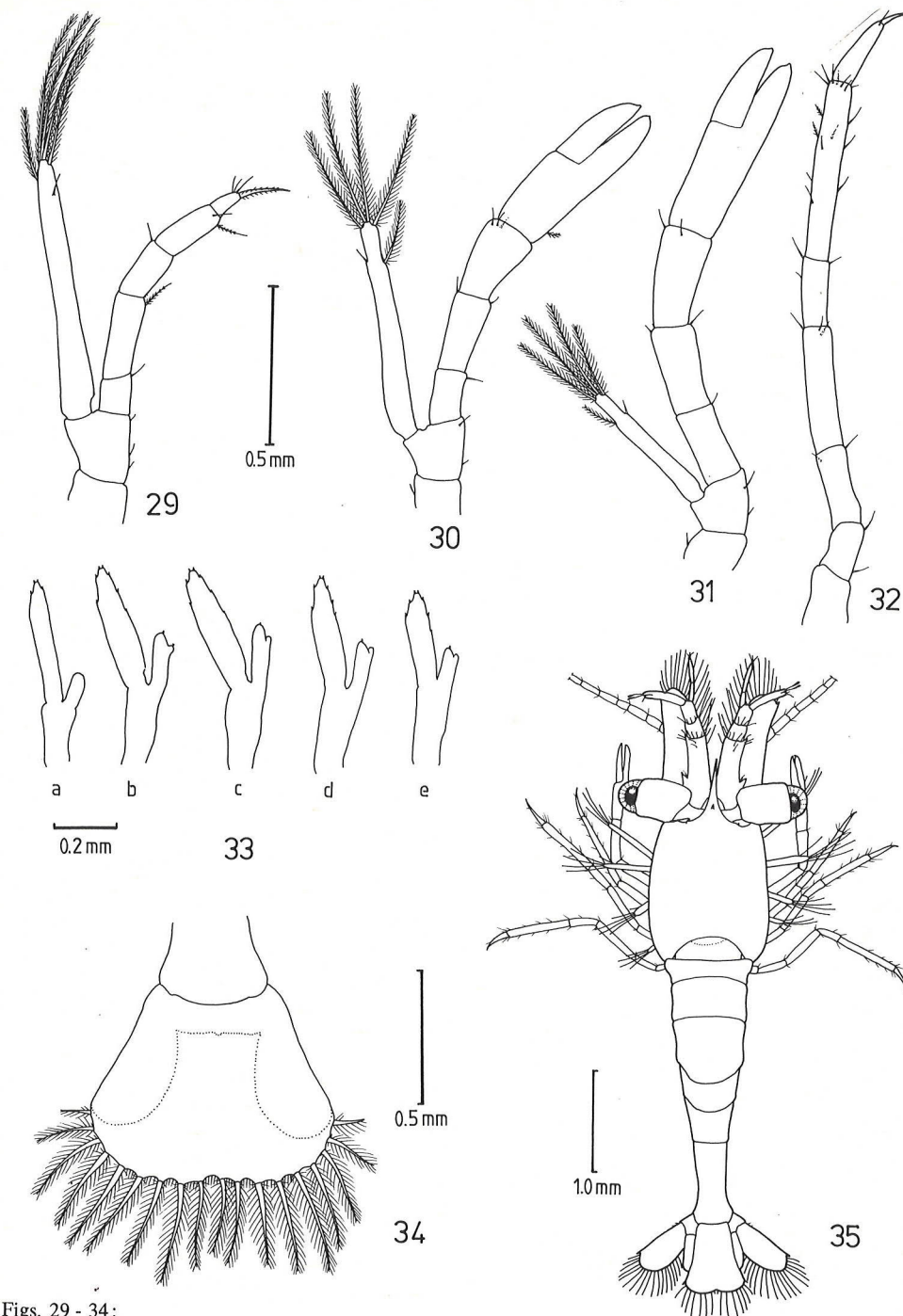
Figs. 11 - 19:

*Palaemonetes ivonicus*, larva I:

11: Maxilliped 2; 12: Maxilliped 3; 13: Pereiopod 1; 14: Pereiopod 2; 15: Pereiopod 3; 16: Pereiopod 4; 17: Pereiopod 5; 18a - e: Pleopods 1 to 5; 19: Telson.

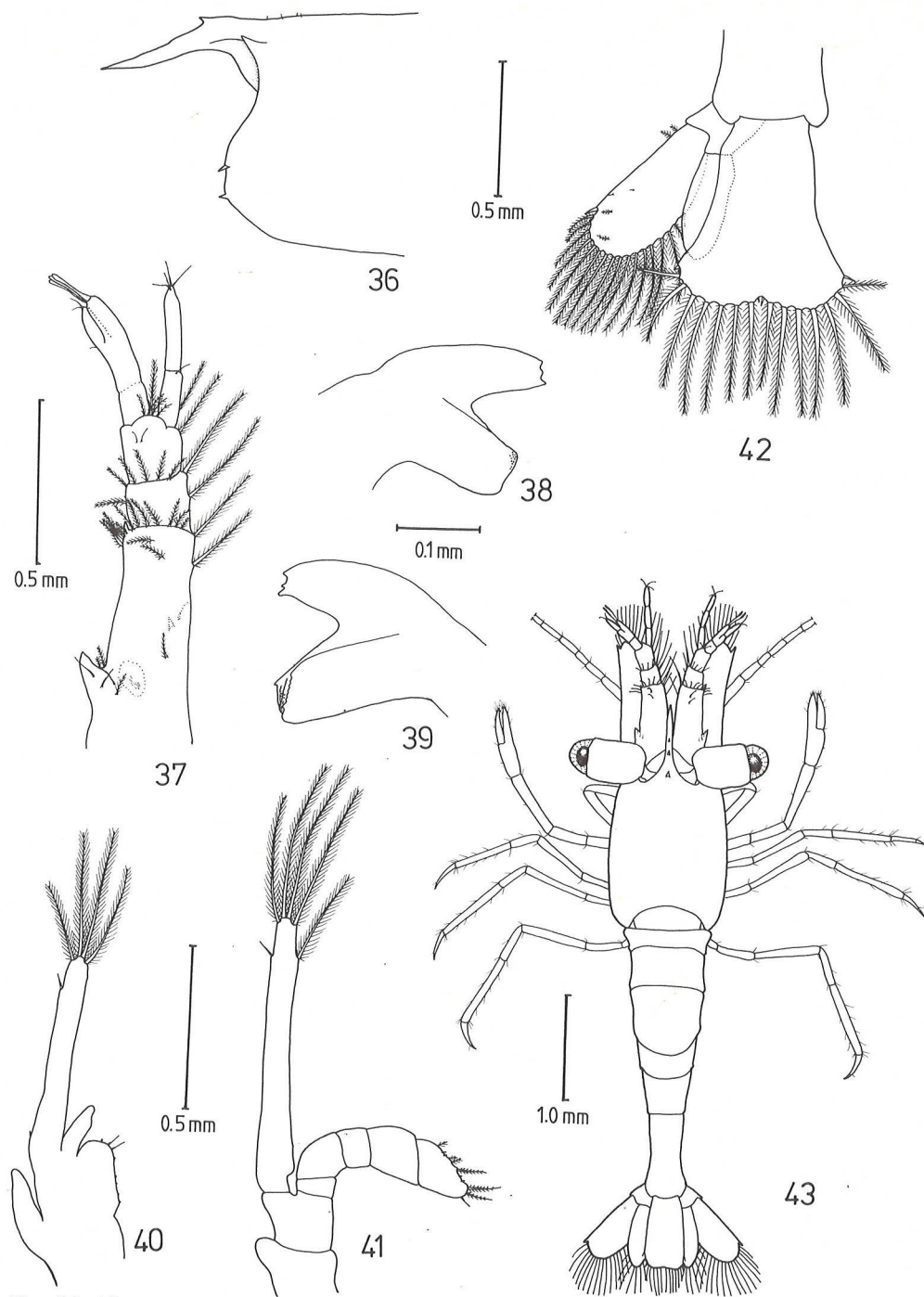


Figs. 20 - 28:  
*Palaemonetes ivonicus*, larva II:  
20: Dorsal view; 21: Lateral view of the anterior part of the carapace; 22: Antennule; 23: Antenna;  
24: Left mandible; 25: Right mandible; 26: Maxillula; 27: Maxilliped 1; 28: Maxilliped 2.

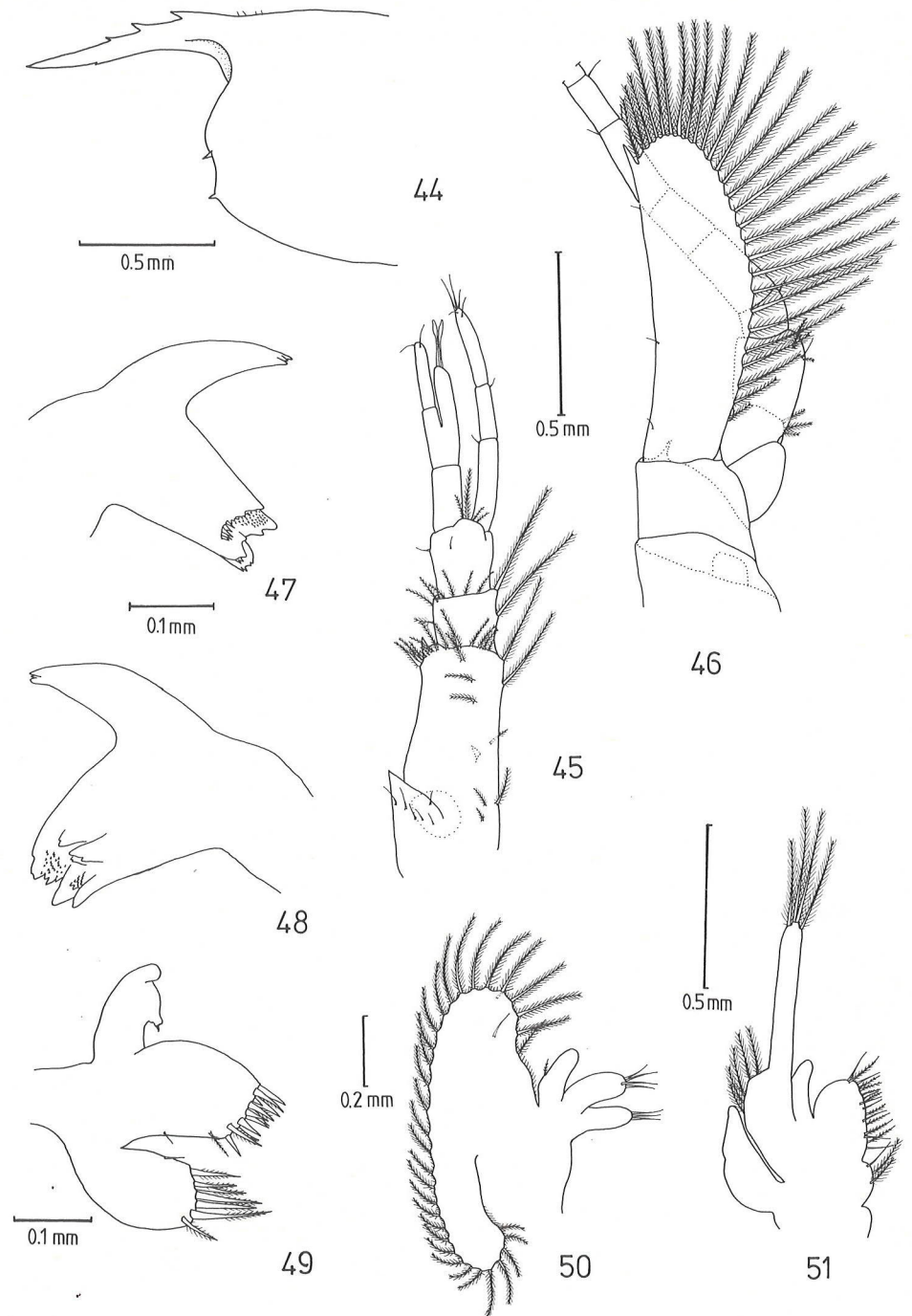


Figs. 29 - 34:  
*Palaemonetes ivonicus*, larva II:  
29: Maxilliped 3; 30: Pereiopod 1; 31: Pereiopod 2; 32: Pereiopod 5; 33a - e: Pleopods 1 to 5; 34: Telson.  
Fig. 35:  
*Palaemonetes ivonicus*, larva III:  
35: Dorsal view.



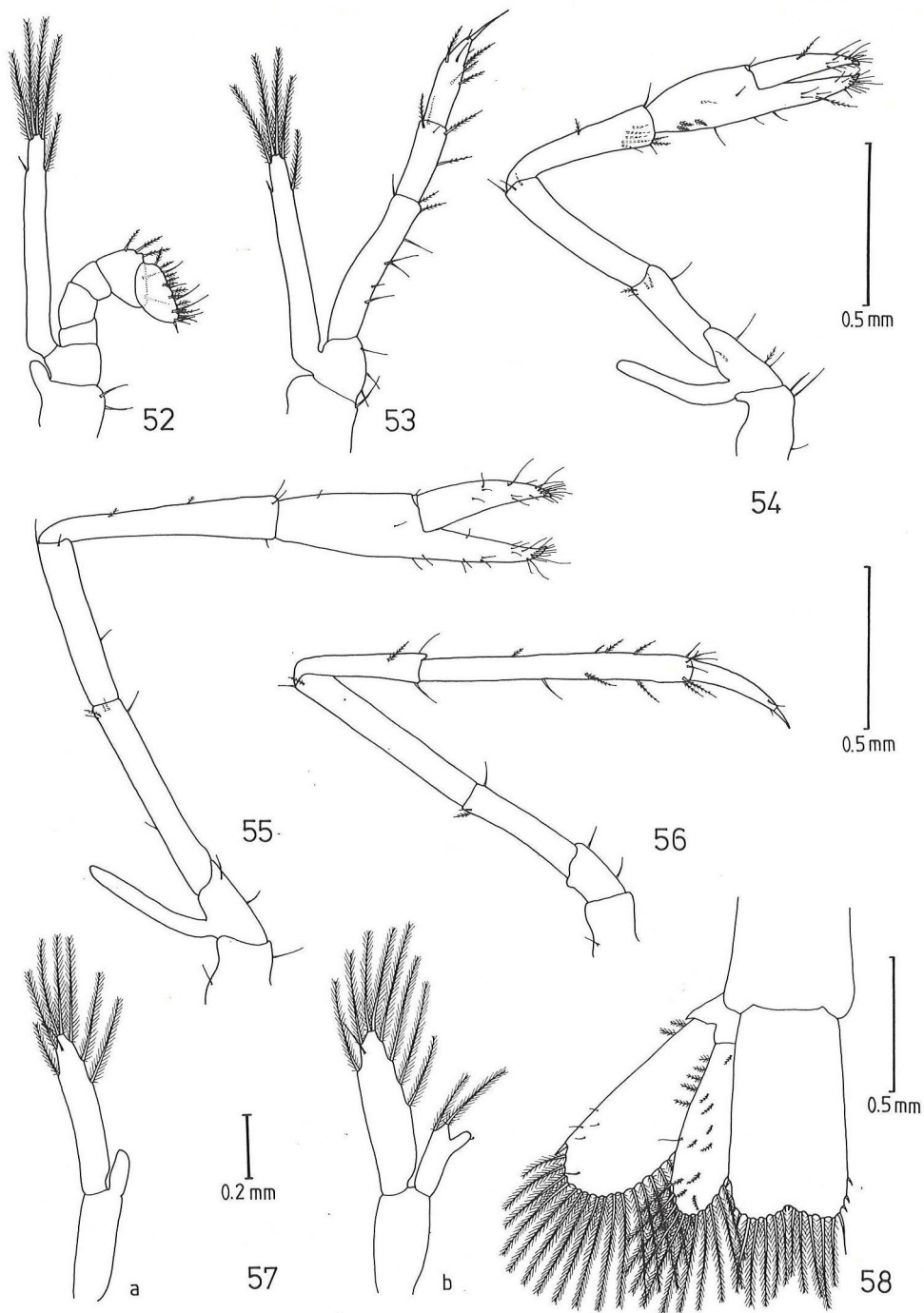


Figs. 36 - 42:  
*Palaemonetes ivonicus*, larva III:  
 36: Lateral view of the anterior part of the carapace; 37: Antennule; 38: Left mandible;  
 39: Right mandible; 40: Maxilliped 1; 41: Maxilliped 2; 42: Left uropod and telson.  
 Fig. 43:  
*Palaemonetes ivonicus*, juvenile I:  
 43: Dorsal view.



Figs. 44 - 51:  
*Palaemonetes ivonicus*, juvenile I:  
 44: Lateral view of the anterior part of the carapace; 45: Antennule; 46: Antenna; 47: Left mandible;  
 48: Right mandible; 49: Maxillula; 50: Maxilla; 51: Maxilliped 1.





Figs. 52 - 58:

*Palaemonetes ivonicus*, juvenile I:

52: Maxilliped 2; 53: Maxilliped 3; 54: Pereiopod 1; 55: Pereiopod 2; 56: Pereiopod 5;  
57a, b: Pereiopod 1 and 3; 58: Left uropod and telson.